

## THE SYNERGISM HYPOTHESIS: A THEORY WHOSE TIME HAS COME

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### Abstract

“The Synergism Hypothesis” is a theory about the rise of complexity in biological evolution. First proposed in 1983, it asserts that cooperative effects of various kinds have been elaborately favored over time by natural selection, and that they have been largely responsible for the progressive evolution of complex organic systems. The biologist John Maynard Smith termed this process “Synergistic Selection.” Over the years this theory has been supported by, among other things, the extensive work on symbiogenesis, the research on evo-devo, (or epigenetic evolution), the many cases of hybridization in evolution, by lateral gene transfer, and especially the extensive evidence of “Lamarckian” evolution via changes in behavior. In recent years, this theory has been significantly augmented by the growing evidence that evolution of the Earth itself over billions of years has been shaped in a co-evolutionary process involving the influence of living systems themselves, including especially cyanobacteria and deciduous plants and trees. Aerobic life is a direct result of this process. Synergistic effects in living systems have had a major causal role in evolution.

**Keywords:** Evolution, complexity, cooperative effects, symbiogenesis, synergistic selection

### 1 | Introduction

“*The Synergism Hypothesis*” is an idea whose time has come. It was first proposed almost half a century ago in a full-length book with this title (Corning, 1983). Although the book garnered some significant support when it was first published (see the summary in Corning, 2011), it did not obtain reviews from major science journals. In short, The Synergism Hypothesis was launched on an unfavorable political tide. In the 1970s and early 1980s, the sociobiology controversy was underway, along with neo-Darwinism (also referred to as The Modern Synthesis after Julian Huxley’s 1942 book) as well as biologist Richard Dawkins’s influential volume, *The Selfish Gene* (1989/1976). The widespread assumption back then was that evolution was a gene-centered, individualistic, competitive process.

In fact, cooperation was widely viewed in those days as an exception in nature that required extraordinary circumstances – like kin selection (or inclusive fitness) – to account for it. Of course, this overlooked the vast domain of symbiotic phenomena in the natural world, not to mention the many examples of social cooperation among unrelated individuals (which utterly contradicts inclusive fitness theory), as well as the close cooperation among the genes in genomes. Evolution was widely portrayed in the latter 20<sup>th</sup> century as a competitive “struggle for existence” – or the “survival of the fittest” in the terminology of the well-known nineteenth century theorist Herbert Spencer (1892/1852), a term which Darwin also adopted.

Richard Dawkins, in his legendary popular book, *The Selfish Gene*, famously characterized humankind and other living systems as “survival machines – robot vehicles that are blindly programmed to preserve the selfish molecules known as genes” (Dawkins 1989/1976: ix). We now know that this was seriously misleading. Arguably, it is the other way around; genes have evolved in the service of living organisms, for the most part, and the exceptions prove the rule (see Baverstock, 2021; Noble & Noble, 2022, 2023).

Another factor that influenced the reception of the Synergism Hypothesis was the rise of complexity theory in the 1990s. This academic movement, closely associated with the Santa Fe Institute, was fueled by new developments in mathematics, especially chaos theory and dynamical systems theory.

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A number of biophysicists were inspired to search for some underlying law (or laws) of complexity in evolution, an approach that was radically opposed to the Darwinian vision of a contingent, always-at-risk, “trial-and-success” dynamic. Biologist Stuart Kauffman (1995), for instance, wrote eloquently of what he called the “physics of biology” and claimed that “Much of the order found [in nature] is spontaneously present...casting an image of permanence and law over biology...It is emergent order, honored and honed by natural selection.” In other words, there is an inherent trend toward complexity embedded in the physics (and biology) of the universe itself, and no additional explanatory theory is needed. Ultimately, Kauffman’s view did not gain traction, and he has since moved on (e.g., Kauffman, 2019).

But perhaps the most serious problem with the Synergism Hypothesis was the very nature of the idea. Like Darwin’s concept of natural selection, the Synergism Hypothesis is at once very simple but rather subtle. Let me briefly explain.

### 2 | On Natural Selection

Natural selection is actually a metaphor for an important aspect, or property of the ongoing evolutionary process. Darwin's inspiration for his famous term was the artificial selection practiced by animal breeders. Unlike artificial selection, however, natural selection is not an active selecting agency, or a force. It is an umbrella concept that refers to whatever functionally significant factors, as opposed to historical contingencies, fortuitous effects, or physical laws, are responsible in any given context for causing differential survival and reproduction. Properly conceptualized, these causal factors are always relational; they are defined both by an organism and its environment(s), and by the interactions between them.

Hence, one cannot technically speak of selective "mechanisms" or fix on a particular "selection pressure" for the workings of natural selection; these are only shorthand expressions. Rather, one must focus on the interactions that occur within an organism and between an organism and its environment(s), inclusive of other organisms. Natural selection as a *causal agency*, in other words, refers to the *functional consequences* produced by adaptively significant changes in any given organism-environment relationship – that is, the bioeconomic payoffs in relation to survival and reproduction (Corning, 2012).

### 3 | Holistic Darwinism

The Synergism Hypothesis represents an extension of this line of reasoning. I refer to it as Holistic Darwinism (see Corning, 2005) because the focus is on the differential selection of wholes, and the combinations of genes, or individuals, that produce them. Simply stated, cooperative interactions of various kinds, however they may occur, can produce novel combined effects -- synergies -- that in turn become the causes of differential selection. The parts that are responsible for producing the synergies then become interdependent units of evolutionary change.

In other words, it is the bioeconomic payoffs associated with various synergistic effects in a given context that constitute the underlying cause of cooperative relationships and complex organization in nature. The synergy produced by the whole provides the functional benefits that may differentially favor the survival and reproduction of the parts. Although it may seem like backwards logic, the thesis is that functional synergy is the underlying cause of cooperation, and organization, in living systems, not the other way around. So, the Synergism Hypothesis is, in essence, a functional (economic) theory of emergent complexity in evolution, and it applies alike to biological, cultural, economic, and even political evolution. (See Corning, 1983, 2003, 2005, 2012, 2018).

### 4 | Growing Support

Over the more than 40 years since The Synergism Hypothesis was first proposed, the case for a more cooperative model of biological evolution has grown ever stronger. Among other things, there is the extensive evidence, championed especially by biologist Lynn Margulis (1970,1993,1998; Margulis & Fester 1991; Margulis & Sagan 2002), that symbiosis – cooperative relationships between organisms of

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different species with complementary capabilities – is a widespread phenomenon in the natural world and that “symbiogenesis” (a concept first proposed by the little-known Russian theorist A.S. Famintsyn (1907a,b, 1918) has played a major causal role in shaping the evolutionary trajectory over time (see also Sapp, 1994, 2009; Gontier, 2007; Carrapiço, 2010; Archibald, 2014). Symbiogenesis theory shifts the locus of innovation away from random changes in genes, genomes, and the classical, competitive model of natural selection to the purposeful (cooperative) actions of the phenotypes and their functional consequences.

Another challenge to the Modern Synthesis and neo-Darwinism arose with the discovery that single celled prokaryotes are profligate sharers of genetic material via horizontal (or lateral) gene transmission and do not strictly follow the pattern of competition and Mendelian (vertical) inheritance from parent to offspring, as assumed in the Modern Synthesis (Sapp, 2009; Koonin, 2011; Crisp, et al., 2015). As the biologist Eugene Koonin (2009) concluded, all the central tenets of the Modern Synthesis break down with prokaryotes and the findings of comparative genomics. It has been argued that the prokaryote world can best be described as a single, vast, interconnected gene pool.

The rise of evolutionary developmental biology (evo-devo for short) also produced serious challenges to the Modern Synthesis model, including the discovery that there are many deep homologies and highly conserved structural gene complexes in the genome (some of which are universal in living systems), along with the extensive work on morphological development and on “phenotypic plasticity” (Müller & Newman, 2003; West Eberhard, 2003; 2005a, 2005b; Koonin, 2011; Bateson & Gluckman, 2011).

There is also burgeoning evidence that the genome is in fact a “two-way read-write system,” as the biologist James Shapiro (2011, 2013, 2022) characterizes it. The extensive and rapidly increasing evidence of epigenetic inheritance (changes in the phenotype that are transmitted to the germ plasm in the next generation) also falsifies the one-way, gene-centered theory (see also Jablonka, 2013; Jablonka & Raz, 2009; Jablonka & Lamb, 2014; Noble, 2012, 2013, 2015, 2017; 2018; Walsh, 2015; Huneman & Walsh, 2017).

Recent progress in microbiology has also shown that an overwhelming majority of DNA changes in the genome are the product of internal regulatory and control networks, not random mutations and incremental (additive) selection. There is also much evidence of various biases in mutational processes (Stoltzfus 2019). Indeed, rapid genome alteration and restructuring can be achieved by a variety of mobile DNA “modules” -- transposons (McClintock & Moore, 1987), integrons, CRISPRs, retroposons, variable antigen determinants, and more (Craig, 2002; Craig et al., 2015; Sapp, 2009; Shapiro, 2011, 2013, 2022; Koonin, 2011, 2016; Noble, 2017).

It is now also apparent that individual cells have a variety of internal regulatory and control capabilities that can significantly influence cell development and the phenotype. More significant, they may even provide feedback that modifies the genome and affects subsequent generations (Pan & Zhang, 2009; Gladyshev & Arkhipova, 2011; Koonin, 2011; Shapiro, 1991, 2011, 2022; Noble, 2006, 2011, 2017, 2018). Particularly significant are the discoveries related to the influence of exosomes, which resemble Darwin’s speculative ideas of pangenesis and internal migratory “gemmules” (Darwin’s term) in reproduction, as Noble (2019) has pointed out. Exosomes also clearly violate the so-called Weismann Barrier (the assumption that genetic change is only a one-way process).

As Shapiro (2011:2) emphasizes, “The capacity of living organisms to alter their own heredity is undeniable. Our current ideas about evolution have to incorporate this basic fact of life.” Shapiro cites some 32 different examples of what he refers to as “natural genetic engineering,” including immune system responses, chromosomal rearrangements, diversity generating retroelements, the actions of transposons, genome restructuring, whole genome duplication, and symbiotic DNA integration (see also Shapiro, 1988, 2013, 2022).

Likewise, Jablonka & Lamb (2014) identify four distinct “Lamarckian” modes of inheritance: (1) directed adaptive mutations, (2) the inheritance of characters acquired during development and the lifetime of the individual, (3) behavioral inheritance through social learning, and (4) language-based information transmission. All this prompted biologist Kevin Laland and his colleagues to publish two

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major critiques of Mayr's proximate-ultimate dichotomy (Laland et al., 2011, 2013). These critics argue that proximate and ultimate causes are interpenetrated and that the one-way causal model (from proximate to ultimate) associated with the Modern Synthesis and neo-Darwinism should be replaced with one that recognizes a major role for "reciprocal causation" (see also Calcott, 2013a, b; Corning, 2019).

There are also my own extensive publications over the years (nearly 200 papers/articles and some six books) in which I stress the major role of behavior and cooperative effects in evolution (see especially Corning, 1983, 2003, 2005, 2007, 2011, 2012, 2014, 2018, 2020, 2023; Corning & Szathmáry, 2015; Corning et al. eds., 2023.)

### 5 | "Agency" in Evolution

A living system represents a "combination of labor" with an overarching vocation, a means-ends teleonomy. Some contemporary theorists have adopted the concept of "agency" to characterize this defining biological characteristic (e.g., Walsh, 2015; Okasha, 2018). Other theorists have adopted Humberto Maturana and Francisco Varela's concept of "autopoiesis" (e.g., Capra & Luisi, 2014). Agency is a term that is utilized in biology to characterize the ability of a living system to act as an autonomous, self-directed agent – to vary its morphology, its behavior, and its environment in purposeful ways in relation to external or internal (physiological) conditions and goals. Agency in living systems is a product of the evolutionary "trial and success" process, as the biologist Theodosius Dobzhansky called it. (See also Corning, 2023; Corning et al. eds., 2023.)

Indeed, an appreciation of the role of the organism as a self-organized and self-directed agent in evolution can be traced back at least to Jean Baptiste de Lamarck, who proposed that changes in an animal's "habits", stimulated by environmental changes, have been a primary source of evolutionary change over time. Lamarck (1984/1809:114) wrote: "It is not the organs ... of an animal's body that have given rise to its special habits and faculties; but it is, on the contrary, its habits, mode of life and environment that have over the course of time controlled ... the faculties which it possesses." Darwin was receptive to Lamarck's idea, calling it the "use and disuse of parts." He mentioned it no less than 12 times in *The Origin of Species* (1968/1859).

A major turning point came with the two conferences in the 1950s and an edited conference volume on *Behavior and Evolution* (Roe & Simpson, 1958). In a landmark follow-up essay on the subject, Mayr (1960) concluded: "It is now quite evident that ... the evolutionary changes that result from adaptive shifts are often initiated by a change in behavior, to be followed secondarily by a change in structure ... Changes of evolutionary significance are rarely, except on the cellular level, the direct results of mutation pressure ... The selection pressure in favor of the structural modification is greatly increased by a shift to a new ecological niche, by the acquisition of a new habit, or by both." Mayr did not mention Lamarck, but he characterized these Lamarckian behavioral innovations as the "pacemakers" of evolution.

### 6 | "Teleonomy" in Evolution

In fact, the purposeful behavior of living organisms has had a major influence in shaping natural selection and the trajectory of evolution over time (Corning, 2023; Corning et al., eds., 2023). The term "teleonomy" highlights the fact that evolved processes and systems can exert a significant causal influence on the properties and actions of living systems, both in themselves and in others. (I characterize the evolutionary consequences of this dynamic as "teleonomic selection.")

Over the past half a century, research on learning and innovation by living organisms -- from "smart bacteria" to human-tutored apes and playful dolphins -- has greatly increased. In their book on *Animal Traditions*, Avital & Jablonka (2000) list well over 200 different species. (See also Whiten, 2021.) We now know that primitive *E. coli* bacteria, slime molds, *Drosophila* flies, ants, bees, flatworms, laboratory mice, pigeons, guppies, cuttlefish, octopuses, dolphins, gorillas and chimpanzees, among many species, can learn novel responses to novel conditions, via "classical" and "operant" conditioning.

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Innumerable studies have also documented that many species are capable of sophisticated cost-benefit calculations, sometimes involving several variables, including the perceived risks, energetic costs, time expenditures, nutrient quality, resource alternatives, relative abundance, and more. Animals are constantly required to make decisions about habitats, foraging, food options, travel routes, nest sites, even mates. Many of these decisions are under tight genetic control, with "pre-programmed" selection criteria. But many more are also, at least in part, the product of experience, trial-and-error learning, observation and even, perhaps, some insight learning (Corning, 2014, 2018).

In fact, even plants make decisions. In the marine alga *Fucus*, for example, biologists Simon Gilroy and Anthony Trewavas (2001) have found that at least 17 environmental conditions can be sensed, and the information that it collects is then either summed or integrated synergistically as appropriate. Gilroy and Trewavas conclude: "What is required of plant-cell signal-transduction studies...is to account for 'intelligent' decision-making; computation of the right choice among close alternatives" (see also Trewavas, 2014; Gilroy & Trewavas 2021).

A striking example of decision-making in trees can be seen in the so-called whistling thorn acacia (*Vachellia drepanolobium*) in East Africa, which produces hollow galls that provide accommodation and nutrients for symbiotic ants. The ants repay the trees by providing additional defenses against browsers (like elephants and giraffes) with their stingers and formic acid emissions. However, when the trees are not subject to browsers, they may kick out their symbionts and collapse their galls to conserve scarce water and nutrients (Palmer et al., 2008).

Especially important theoretically are the many forms of social learning through "stimulus enhancement", "contagion effects", "emulation", and even some "teaching". Social learning has been documented in many species of animals, from rats to bats, to lions and elephants, as well as some birds and fish and, of course, domestic dogs. For instance, red-wing blackbirds, which readily colonize new habitats, are especially prone to acquire new food habits -- or food aversions -- from watching other birds (Weigl & Hanson, 1980). Pigeons can learn specific food-getting skills from other pigeons (Palameta & LeFebvre, 1985). Domestic cats, when denied the ability to observe conspecifics, will learn certain tasks much more slowly or not at all (John et al., 1968). And, in a controlled laboratory study, naive ground squirrels (*Tamiasciurus hudsonicus*) that were allowed to observe an experienced squirrel feed on hickory nuts were able to learn the same trick in half the time it took for unenlightened animals (cited in Byrne, 1995:58).

True "imitation" (including the learning of motor skills) has also been observed in, among others, gorillas (peeling wild celery to get at the pith), rats (pressing a joy stick for food rewards), African grey parrots (vocalizations and gestures), chimpanzees (nut-cracking with an anvil and a stone or wooden hammer), and bottlenose dolphins (many behaviors, including grooming, sleeping postures, even mimicking the divers that scrape the observation windows of their pools and the sounds made by the divers' breathing apparatus) (see Corning, 2014).

Not surprisingly, the most potent cognitive skills have been found in social mammals, especially the great apes. They display intentional behavior, planning, social coordination, understanding of cause and effect, anticipation, generalization, even deception. Primatologists Richard Byrne and Andrew Whiten, in their two important edited volumes on the subject, referred to it as "Machiavellian intelligence" (Byrne & Whiten, 1988; Whiten & Byrne, 1997; also, Gibson & Ingold, 1993; de Waal, 2016; Whiten, 2021). Cognitive skills and social learning have provided a powerful means -- which humankind has greatly enhanced -- for accumulating, dispersing and perpetuating novel adaptations without waiting for slower-acting genetic changes to occur.

Tool-use is an especially significant and widespread category of adaptive behavior in the natural world -- from insects to insectivores and omnivores -- and it is utilized for a wide variety of purposes. As Edward O. Wilson (1975) pointed out in his comprehensive survey and synthesis, *Sociobiology*, tools provide a means for quantum jumps in behavioral invention, and in the ability of living organisms to manipulate their environments. Tool-using synergies can result in otherwise unattainable behavioral outcomes (Wilson, 1975:172; also, Beck, 1980; McGrew, 1992; Wrangham et al., 1994).

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It is also important to take note of the role of “culture” and cultural transmission in evolutionary change. The evidence continues to mount that cultural influences are present in many species – from primates to cetaceans, birds, fish, whales, even some insects (see Whiten 2021). Of course, culture has played an especially important role in shaping human evolution (see Corning, 2003, 2012, 2018; also, Kingdon, 1993; Foley, 1995; Klein, 1999; Klein & Edgar, 2002; Boyd & Richerson, 2005, 2009; Richerson & Boyd, 2005; Boyd et al., 2011, 2013; Foley & Gamble, 2011; Henrich, 2016; Richerson et al., 2021; Whiten, 2021; Waring & Wood, 2021).

### 7 | The Co-Evolution of The Earth and Life

Finally, we have learned from sophisticated research over the past several years regarding the history of the Earth that biological evolution and the evolution of the Earth’s environment over the past 4.5 billion years has involved a synergistic, co-evolutionary process. Our oceans, covering 70 percent of the Earth’s surface and vital to sustaining life, were first formed from trillions of water droplets that condensed from the Earth’s early atmosphere. Although there remains uncertainty about the locus of what has been called “the great oxidation event” which produced our earliest oxygenated atmosphere, it is increasingly evident that life itself was responsible, in the form of primitive cyanobacteria in the trillions that drew energy from the sun (photosynthesis), consumed carbon dioxide, and produced oxygen as a byproduct. Likewise, the Earth’s current atmosphere, which sustains the proliferation of aerobic organisms on Earth – including humankind – was made possible by the rise of trillions of photosynthesizing, oxygen producing, plants and trees (NOVA TV, Series 50, Episodes 13-15).

### 8 | Conclusion

It is now quite evident that synergies of many different kinds have played a key role in the ongoing evolution of the Earth itself and in the rise of its many diverse forms of life via a long co-evolutionary process. Going forward it will be up to our species to preserve it, or not. We shall see.

### References

- Archibald, J. 2014. *One Plus One Equals One: Symbiosis and the Evolution of Complex Life*. Oxford: Oxford University Press.
- Avital, E., E. Jablonka. 2000. *Animal Traditions: Behavioral Inheritance in Evolution*. Cambridge, UK: Cambridge University Press.
- Bateson, P.P.G., P. Gluckman. 2011. *Plasticity, Robustness, Development, and Evolution*. Cambridge, UK: Cambridge University Press.
- Baverstock, K. 2021. “The gene: An appraisal.” *Progress in Biophysics and Molecular Biology*, [Doi.org/10.1016/j.pbiomolbio.2021.04.005](https://doi.org/10.1016/j.pbiomolbio.2021.04.005)
- Beck, B.B. 1980. *Animal Tool Behavior*. New York, NY: Garland Press.
- Boyd, R., P.J. Richerson, J. Henrich. 2011. “The cultural niche: Why social learning is essential for human adaptation.” *Proceedings of the National Academy of Sciences of the United States of America* 108:10918-10925.
- Boyd, R., P.J. Richerson, J. Henrich. 2013. “Cultural evolution of technology: Facts and theories.” In *Cultural Evolution: Society, Technology, Language, and Religion*, edited by P. J. Richerson, and M. Christiansen, 119-142. Cambridge, MA: MIT Press.
- Boyd, R., P.J. Richerson. 2005. *The Origin and Evolution of Cultures*. Oxford: Oxford University Press.
- Boyd, R., P.J. Richerson. 2009. “Culture and the evolution of human cooperation.” *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 364: 3281–3288.

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- Byrne, R.W. 1995. *The Thinking Ape: Evolutionary Origins of Intelligence*. Oxford: Oxford University Press.
- Byrne, R.W., A. Whiten. 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Oxford University Press.
- Calcott B. 2013b. “Why how and why aren't enough: More problems with Mayr's proximate-ultimate distinction. *Biology and Philosophy* 28(5): 767-780.
- Calcott, B. 2013a. “Why the proximate–ultimate distinction is misleading, and why it matters for understanding the evolution of cooperation.” In: *Cooperation and its evolution*, edited by K. Sterelny, R. Joyce, B. Calcott, and B. Fraser, 249-263. Cambridge, MA: MIT Press.
- Capra, F., P.L. Luisi. 2014. *The Systems View of Life: A Unifying Vision*. Cambridge, UK: Cambridge University Press.
- Carrapiço, F. 2010. “How symbiogenic is evolution?” *Theoretical Bioscience* 129: 135
- Corning P.A., S.A. Kauffman, D. Noble, J.A. Shapiro, R.I. Vane-Wright, A. Pross eds. 2023b. *Evolution “On Purpose”: Teleonomy in Living Systems*. Cambridge, MA. The MIT Press.
- Corning, P.A. 1983. *The Synergism Hypothesis: A Theory of Progressive Evolution*. New York: McGraw Hill.
- Corning, P.A. 2003. *Nature's Magic: Synergy in Evolution and the Fate of Humankind*. Cambridge, UK: Cambridge University Press.
- Corning, P.A. 2005. *Holistic Darwinism: Synergy, Cybernetics and the Bioeconomics of Evolution*. Chicago, IL: University of Chicago Press.
- Corning, P.A. 2007. “Control Information Theory: The ‘missing link’ in the Science of Cybernetics.” *Systems Research and Behavioral Science* 24: 297-311.
- Corning, P.A. 2011. “‘The Synergism Hypothesis’ thirty years later. *Politics and the Life Sciences* 30(1): 61-64.
- Corning, P.A. 2012. “Rotating the Necker cube: A bioeconomic approach to cooperation and the causal role of synergy in evolution.” *Journal of Bioeconomics* DOI: [10.1007/s10818-0129142-4](https://doi.org/10.1007/s10818-0129142-4).
- Corning, P.A. 2014. “Evolution ‘On Purpose’: How behaviour has shaped the evolutionary process.” *Biological Journal of the Linnean Society* 112: 242-260.
- Corning, P.A. 2018. *Synergistic Selection: How Cooperation Has Shaped Evolution and the Rise of Humankind*. Singapore, London, New Jersey: World Scientific.
- Corning, P.A. 2019. “Teleonomy and the proximate-ultimate distinction revisited.” *Biological Journal of the Linnean Society* 127(4): 912–916. DOI: [10.1093/biolinnean/blz087](https://doi.org/10.1093/biolinnean/blz087)
- Corning, P.A. 2020. “Beyond the Modern Synthesis: A framework for a more inclusive biological synthesis.” *Progress in Biophysics and Molecular Biology* 153: 5-12. DOI.org/[10.1016/j.pbiomolbio.2020.02.002](https://doi.org/10.1016/j.pbiomolbio.2020.02.002)
- Corning, P.A. 2023. “Teleonomy in evolution: ‘The Ghost in the Machine.’” In Corning P.A., S.A. Kauffman D. Noble, J.A. Shapiro, R.I. Vane-Wright, A. Pross eds. *Evolution “On Purpose”: Teleonomy in Living Systems*. Cambridge, MA. The MIT Press.
- Corning, P.A., Szathmáry, E. 2015. ‘Synergistic selection’: A Darwinian frame for the evolution of complexity.” *Journal of Theoretical Biology* 371: 45-58.
- Craig, N.L. 2002. *Mobile DNA II*. Washington, D.C.: American Society for Microbiology Press.
- Craig, N.L. M. Chandler, A. Gellert, A. Lambowitz, P.A., Rice, eds. 2015. *Mobile DNA III*. American Society for Microbiology, Washington, D.C.
- Crisp, A., C. Boschetti, M. Perry, A. Tunnacliffe, G. Micklem 2015. “Expression of multiple horizontally acquired genes is a hallmark of both vertebrate and invertebrate genomes.” *Genome Biology*, 16: 50. DOI:[10.1186/s13059-015-0607-3](https://doi.org/10.1186/s13059-015-0607-3)

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- Darwin, C.R. 1968/1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. Baltimore, MD: Penguin.
- Dawkins, R. 1989/1976. *The Selfish Gene*. New York: Oxford University Press.
- de Waal, F. 2016. *Are We Smart Enough to Know How Smart Animals Are?* New York: W.W. Norton.  
DOI: [10.1126/science.aba3776](https://doi.org/10.1126/science.aba3776)  
DOI: [10.1152/physiol.00017.2018](https://doi.org/10.1152/physiol.00017.2018).
- Famintsyn, A.S. 1907a. “Concerning the role of symbiosis in the evolution of organisms.” *Mémoires Acad. Sci., Ser. 8, Physical-Mathematical Division* 20(3):1-14. (in Russian)
- Famintsyn, A.S. 1907b. “Concerning the role of symbiosis in the evolution of organisms.” *Transactions of the St. Petersburg Society of Natural Science, 38(1), Minutes of Session, 4*: 141-143. (in Russian)
- Famintsyn, A.S. 1918. “What is going on with Lichens?” *Nature* (April-May): 266-282.
- Foley, R. 1995. *Humans before Humanity: An Evolutionary Perspective*. Oxford: Blackwell.
- Foley, R., C. Gamble. 2011. “The ecology of social transitions in human evolution.” *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 364: 3267– 3279.
- Gibson, R., T. Ingold, eds. 1993. *Tools, Language, and Cognition in Human Evolution*. Cambridge, UK: Cambridge University Press.
- Gilroy, S., A. Trewavas. 2001. “Signal processing and transduction in plant cells: The end and the beginning.” *Nature Reviews (Molecular Cell Biology)* 2: 307–314.
- Gilroy, S., A. Trewavas. 2021. “Agency, teleonomy and signal transduction in plant systems. In Corning P.A., S.A. Kauffman D. Noble, J.A. Shapiro, R.I. Vane-Wright, A. Pross eds. *Evolution “On Purpose”: Teleonomy in Living Systems*. Cambridge, MA. The MIT Press.
- Gladyshev, E.A., I.R. Arkhipova. 2011. “A widespread class of reverse transcriptase-related cellular genes”. *Proceedings of the National Academy of Sciences of the United States of America* 108 (51): 20311-20316. [Doi.org/10.1073/pnas.1100266108](https://doi.org/10.1073/pnas.1100266108).
- Gontier, N. 2007. “Universal symbiosis: An alternative to universal selectionist accounts of evolution.” *Symbiosis* 44: 167–181.
- Henrich, J. 2016. *The Secret of our Success: How Culture is Driving Human Evolution, Domesticating our Species, and Making us Smarter*. Princeton, N.J. and Oxford: Princeton University Press.
- Huneman, P., D.M. Walsh 2017. *Challenging the Modern Synthesis: Adaptation, Development, and Inheritance*. New York: Oxford University Press.
- Huxley, J.S. 1942. *Evolution: The Modern Synthesis*. New York: Harper & Row.
- Jablonka, E. 2013. “Epigenetic inheritance and plasticity: The responsive germline.” *Progress in Biophysics and Molecular Biology* 111: 99-107. DOI: [10.1016/j.pbiomolbio.2012.08.014](https://doi.org/10.1016/j.pbiomolbio.2012.08.014).
- Jablonka, E., G. Raz, 2009. “Transgenerational epigenetic inheritance: Prevalence, mechanisms, and implications for the study of heredity and evolution.” *Quarterly Review of Biology* 84(2): 131-176. DOI: [10.1086/598822](https://doi.org/10.1086/598822).
- Jablonka, E., M.J. Lamb, 2014. *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life* (rev. edn.). Cambridge, MA.: MIT Press.
- John, E.R., P. Chesler, F. Bartlett, I. Victor. 1968. “Observation learning in cats.” *Science* 159: 1489–1491.
- Kauffman, S.A. 1995. *At Home in the Universe: The Search for the Laws of Self-Organization and Complexity*. New York: Oxford University Press.
- Kauffman, S.A. 2019. *A World Beyond Physics. The Emergence & Evolution of Life*. New York: Oxford University Press.
- Kingdon, J. 1993. *Self-made Man: Human Evolution from Eden to Extinction?* New York: John Wiley.

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- Klein, R.G. 1999. *The Human Career: Human Biological and Cultural Origins (2nd edn.)*. Chicago, IL: University of Chicago Press.
- Klein, R.G., B. Edgar. 2002. *The Dawn of Human Culture*. New York: John Wiley & Sons.
- Koonin, E.V. 2011. *The Logic of Chance: The Nature and Origin of Biological Evolution*. Upper Saddle River, NJ: FT Press, Science.
- Koonin, E.V. 2016. Viruses and mobile elements as drivers of evolutionary transitions. *Philosophical Transactions of the Royal Society of London, Series B* 371: 20150442. DOI: [10.1098/rstb.2015.0442](https://doi.org/10.1098/rstb.2015.0442)
- Koonin, E.V. 2009. “The Origin at 150: Is a new evolutionary synthesis in sight?” *Trends in Genetics* 25(11): 473–475. DOI:[10.1016/j.tig.2009.09.007](https://doi.org/10.1016/j.tig.2009.09.007).
- Laland, K.N., F.J. Odling-Smee, W. Hoppitt, T. Uller. 2013. “More on how and why: Cause and effect in biology revisited.” *Biology and Philosophy* 28(5): 719-745.
- Laland, K.N., K. Sterelny, F.J. Odling-Smee, W. Hoppitt, T. Uller. 2011. “Cause and effect in biology revisited: Is Mayr’s proximate-ultimate dichotomy still useful?” *Science* 334: 1512-1516.
- Lamarck, J-B. 1984/1809. *Zoological Philosophy: An Exposition with Regard to the Natural History of Animals* (Elliot, H. trans.). Chicago, IL: University of Chicago Press.
- Margulis, L. 1970. *Origin of Eukaryotic Cells*. New Haven, CT: Yale University Press.
- Margulis, L. 1993. *Symbiosis in Cell Evolution (2<sup>nd</sup> ed.)*. New York: W.H. Freeman.
- Margulis, L. 1998. *Symbiotic Planet: A New Look at Evolution*. New York: Basic Books.
- Margulis, L., D. Sagan. 2002. *Acquiring Genomes: A Theory of the Origins of Species*. New York: Basic Books.
- Margulis, L., R. Fester, eds. 1991. *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis*. Cambridge, MA: MIT Press.
- Mayr, E. 1960. “The emergence of evolutionary novelties.” In S. Tax ed., *Evolution after Darwin* (Vol I): 349-380. Chicago, IL: University of Chicago Press.
- McClintock, B., J.A. Moore, eds. 1987. *The Discovery and Characterization of Transposable Elements: The Collected Papers of Barbara McClintock*. New York: Garland Publishers.
- McGrew, W.C. 1992. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge, UK: Cambridge University Press.
- Müller, G.B., S.A. Newman, eds. 2003. *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*. Cambridge, MA: MIT Press.
- Noble D, R. Noble, 2022 “Origins and demise of selfish gene theory.” *Theoretical Biology Forum* 115 (1-2): 29-43.
- Noble, D, R. Noble, R. “Origins and demise of selfish gene theory.” *Theoretical Biology Forum* (in press).
- Noble, D. 2006. *The Music of Life: Biology Beyond the Genes*. Oxford: Oxford University Press.
- Noble, D. 2011. “Neo-Darwinism, the modern synthesis and selfish genes: Are they of use in physiology?” *Journal of Physiology* 589 (5): 1007–1015. DOI:[10.1111/ophysiol.2010.20](https://doi.org/10.1111/ophysiol.2010.20)
- Noble, D. 2012. “A theory of biological relativity: No privileged level of causation.” *Interface Focus* 2: 55-64.
- Noble, D. 2013. “Physiology is rocking the foundations of evolutionary biology. *Experimental Physiology* 98(8): 1235-1243. DOI: [10.1113/expphysiol.2012.071134](https://doi.org/10.1113/expphysiol.2012.071134).
- Noble, D. 2015. “Evolution beyond neo-Darwinism: A new conceptual framework.” *Journal of Experimental Biology* 218 (Pt 1): 7–13. DOI: [10.1242/jeb.106310](https://doi.org/10.1242/jeb.106310).
- Noble, D. 2017. *Dance to the Tune of Life: Biological Relativity*. Cambridge, UK: Cambridge University Press.

## The Synergism Hypothesis

- Noble, D. 2018. “Central dogma or central debate?” *Physiology* 33: 246-249.
- Noble, D. 2019. “Exosomes, gemmules, pangenes, and Darwin. In *Exosomes: A Clinical Compendium*, edited by L.R. Edelman, J.R. Smythies, P.J. Quesenberry, D. Noble, 487-501. Amsterdam: Elsevier.
- Noble, R. Noble, D. 2023. *Understanding Living Systems*. Cambridge, UK: Cambridge University Press.
- Okasha, S. 2018. *Agents and Goals in Evolution*. Oxford: Oxford University Press.
- Palameta, B., L.K. Lefebvre. 1985. “The social transmission of a food-finding technique in pigeons: What is learned?” *Animal Behaviour* 33: 892-896.
- Palmer, T.M., M.L. Stanton, T.P. Young, J.R. Goheen, R.M. Pringle, R. Karban. 2008. “Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African
- Pan, D., L. Zhang. 2009. “Burst of young retrogenes and independent retrogene formation in mammals.” *PLoS One* 4 (3): e5040. [Doi.org/10.1371/journal.pone.0005040](https://doi.org/10.1371/journal.pone.0005040).
- Richerson, P.J., R. Boyd. 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago, IL: University of Chicago Press.
- Richerson, P.J., S. Gavrilets, F.B.M. de Waal, (2021). Modern theories of human evolution foreshadowed by Darwin’s *Descent of Man*. *Science* 372, eaba3776 (2021).
- Roe, A., G.G. Simpson, eds. 1958. *Behavior and Evolution*. New Haven, CT: Yale University Press.
- Sapp, J. 1994. *Evolution by Association: A History of Symbiosis*. New York: Oxford University Press.
- Sapp, J. 2009. The New Foundations of Evolution, on the Tree of Life. Oxford: Oxford University Press.
- savanna.” *Science* 319 (5860): 192–195. [Doi.org/10.1126/science.1151579](https://doi.org/10.1126/science.1151579)
- Shapiro J.A. 2022. *Evolution: A View from the 21st Century*. Fortified. (2<sup>nd</sup> Edn.) Upper Saddle River, NJ.: FT Science Press.
- Shapiro, J.A. 1988. “Bacteria as multicellular organisms.” *Scientific American* 258: 82–89.
- Shapiro, J.A. 1991. “Genomes as smart systems.” *Genetica* 84: 3–4.
- Shapiro, J.A. 2011. *Evolution: A View from the 21st Century*. Upper Saddle River, NJ.: FT Science Press.
- Shapiro, J.A. 2013. “How life changes itself: The read-write (rw) genome.” *Physics of Life Reviews* 10: 287-323.
- Spencer, H. 1892/1852. The development hypothesis. In *Essays, Scientific, Political, and Speculative*. New York: Appleton.
- Stoltzfus, A. 2019. “Understanding bias in the introduction of variation as an evolutionary cause.” In T. Uller, K.N. Laland, eds. *Evolutionary Causation: Biological and Philosophical Reflections*, 29-61. Cambridge, MA: The MIT Press.
- Trewavas, A. 2014. *Plant Behaviour and Intelligence*. Oxford: Oxford University Press.
- Walsh, D.M. 2015. *Organisms, Agency, and Evolution*. Cambridge, UK: Cambridge University Press.
- Waring, T.M., Z.T. Wood. 2021. “Long-term gene-culture coevolution and the human evolutionary transition.” *Proceedings of the Royal Society, B* 288: 20210538. [Doi.org/10.1098/rspb.2021.0538](https://doi.org/10.1098/rspb.2021.0538)
- Weigl, P.D., E.V. Hanson. 1980. “Observational learning and the feeding behavior of the red squirrel *Tamiasciurus hudsonicus*: The ontogeny of optimization.” *Ecology* 61: 213–218.
- West-Eberhard, M.J. 2003. *Developmental Plasticity and Evolution*. Oxford: Oxford University Press
- West-Eberhard, M.J. 2005a. “Developmental plasticity and the origin of species differences.” *Proceedings of the National Academy of Sciences of the United States of America*. 102 (Suppl. 1), 6543-6549. [DOI.org/10.1073/pnas.0501844102](https://doi.org/10.1073/pnas.0501844102).
- West-Eberhard, M.J. 2005b. “Phenotypic accommodation: Adaptive innovation due to phenotypic plasticity.” *Journal of Experimental Zoology* 304B: 610–618.

## The Synergism Hypothesis

- Whiten, A. 2021. “The burgeoning reach of animal culture.” *Science* 372(6537) [Doi: 10.1126/science.abe6514](https://doi.org/10.1126/science.abe6514)
- Whiten, A., R.W. Byrne. 1997. *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge, UK: Cambridge University Press.
- Wilson, E.O. 1975. *Sociobiology: The New Synthesis*. Cambridge, MA: Harvard University Press.
- Wrangham, R.W., W.C. McGrew, F.B.M. de Waal, P.G. Heltne, eds. 1994. *Chimpanzee Cultures*. Cambridge, MA: Harvard University Press.